High mountain origin, phylogenetics, evolution, and niche conservatism of arctic lineages in the hemiparasitic genus Pedicularis (Orobanchaceae)

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Abstract: The origin of the arctic flora covering the northernmost treeless areas is still poorly understood. Arctic plants may have evolved in situ or immigrated from the adjacent ecosystems. Frequently arctic species have disjunctive distributions between the Arctic and high mountain systems of the temperate zone. This pattern may result from long distance dispersal or from glacial plant migrations and extinctions of intermediate populations. The hemiparasitic genus Pedicularis is represented in the Arctic by c. 28 taxa and ranks among the six most species-rich vascular plant genera of this region. In this study, we test the hypothesis that these lineages evolved from predecessors occurring in northern temperate mountain ranges, many of which are current centers of diversity for the genus. We generated a nuclear ribosomal and chloroplast DNA phylogeny including almost all of the arctic taxa and nearly half of the genus as a whole. The arctic taxa of Pedicularis evolved 12-14 times independently and are mostly nested in lineages that otherwise occur in the high mountains of Eurasia and North America. It appears that only three arctic lineages arose from the present-day center of diversity of the genus, in the Hengduan Mountains and Himalayas. Two lineages are probably of lowland origin. Arctic taxa of Pedicularis show considerable niche conservatism with respect to soil moisture and grow predominantly in moist to wet soils. The studied characteristics of ecology, morphology, and chromosome numbers of arctic Pedicularis show a heterogeneous pattern of evolution. The directions of morphological changes among the arctic lineages show opposing trends. Arctic taxa are chiefly diploid, the few tetraploid chromosome numbers of the genus were recorded only for arctic taxa. Five arctic Pedicularis are annuals or biennials, life forms otherwise rare in the Arctic. Other genera of the Orobanchaceae consist also of an elevated number of short-lived species, thus hemiparasitism may favor this life form in the Arctic.

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ABSTRACT

The origin of the arctic flora covering the northernmost treeless areas is still poorly understood. Arctic plants may have evolved *in situ* or immigrated from the adjacent ecosystems. Frequently arctic species have disjunctive distributions between the Arctic and high mountain systems of the temperate zone. This pattern may result from long distance dispersal or from glacial plant migrations and extinctions of intermediate populations. The hemiparasitic genus *Pedicularis* is represented in the Arctic by c. 28 taxa and ranks among the six most species-rich vascular plant genera of this region. In this study, we test the hypothesis that these lineages evolved from predecessors occurring in northern temperate mountain ranges, many of which are current centers of diversity for the genus. We generated a nuclear ribosomal and chloroplast DNA phylogeny including almost all of the arctic taxa and nearly half of the genus as a whole. The arctic taxa of *Pedicularis* evolved 12–14 times independently and are mostly nested in lineages that otherwise occur in the high mountains of Eurasia and North America. It appears that only three arctic lineages arose from the present-day center of diversity of the genus, in the Hengduan Mountains and Himalayas. Two lineages are probably of lowland origin. Arctic taxa of *Pedicularis* show considerable niche conservatism with respect to soil moisture and grow predominantly in moist to wet soils. The studied characteristics of ecology, morphology, and chromosome numbers of arctic *Pedicularis* show a heterogeneous pattern of evolution. The directions of morphological changes among the arctic lineages show opposing trends. Arctic taxa are chiefly diploid, the few tetraploid chromosome numbers of the genus were recorded only for arctic taxa. Five arctic *Pedicularis* are annuals or biennials, life forms otherwise rare in the Arctic. Other genera of the Orobanchaceae consist also of an elevated number of short-lived species, thus hemiparasitism may favor this life form in the Arctic.

1. Introduction

The Arctic is a large, but young biome, of which major parts were repeatedly devastated by Pleistocene glaciations. It provides an excellent setting for studying, for example, range shifts, speciation and polyploidy. It is of interest to the study of plant evolution because its extreme environmental conditions require responses like adaptation to seasonality, and freezing and desiccation tolerance. Furthermore, this area is strongly affected by global change, thus of nature protection concern. Altogether, c. 2800 vascular plant species and subspecies presently occur in the Arctic, and are considered "arctic" species if their whole (arctic endemics) or only a part of their ranges are situated in the arctic biome (Fig. 1; Panarctic Flora, Elven et al., 2011). The now treeless and cold region of the Arctic (Fig. 1) was covered during much of the Tertiary with deciduous and coniferous forests (e.g., Mai, 1995; Murray, 1995). In the late Tertiary and the ice ages of the Quaternary, cooling and the retreat of the forests created new habitats available for colonisation by plants, especially herbaceous lineages that were able to tolerate or adapt to the harsh environmental condition. Evidence of early arctic vegetation composition based on fossil deposits is confined to a rather limited number of taxa (e.g., *Cerastium*, *Draba*, *Dryas*, *Ranunculus*, *Saxifraga*, *Silene*, *Stellaria*; Bennike and Bøcher, 1990; Bennike et al., 2010; Matthews and Ovenden, 1990). Floristic analyses have suggested that the present

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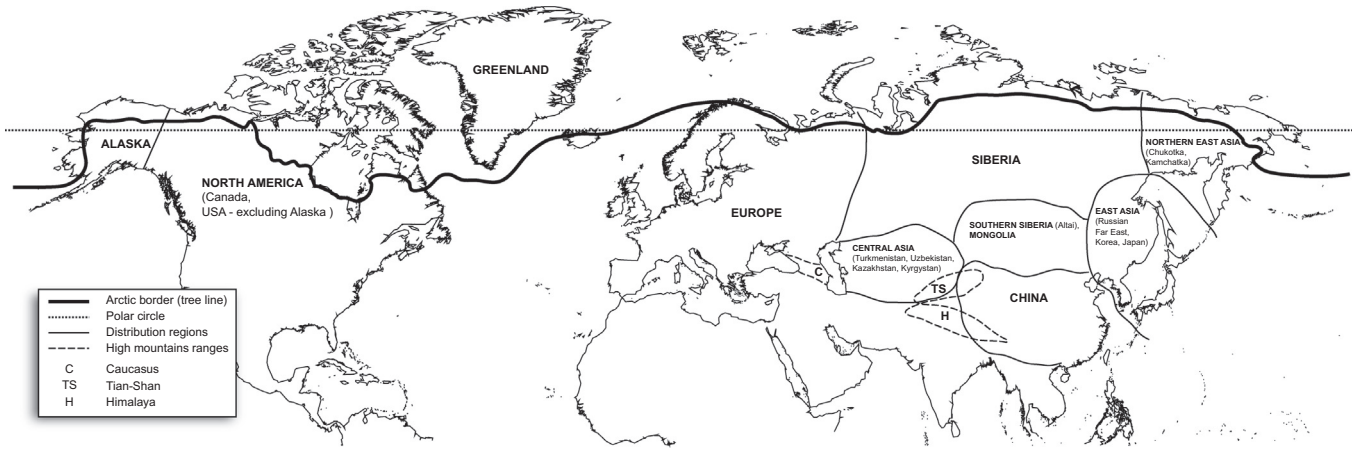

Fig. 1. Delineation of the Arctic following the Panarctic Flora (Elven et al., 2011) and geographical regions outside of the arctic region that are used in this study to circumscribe the southerly distribution of *Pedicularis* taxa. The selection of these arbitrary geographical regions follows the availability of distribution data in various sources explored for this study (see Section 2 for details).

arctic flora originated from different sources, including autochthonous elements of the Arcto-Tertiary vegetation that evolved *in situ* by adapting to the increasingly cold climate, Quaternary migrants from adjacent forests and saline coastal habitats that may have been pre-adapted to arctic conditions and migrants from more remote southern mountains (Tolmachev, 1960, for example, *Salix*, *Carex*, *Potentilla*, and *Saxifraga*).

Phylogeographic studies provided information on postglacial plant migration and re-colonization, northern refugia during the last glacial maximum, and genetic diversity in arctic species (e.g., Abbott and Brochmann, 2003; Allen et al., 2012; Alsos et al., 2005, 2007, 2009; Brochmann and Brysting, 2008; Brochmann et al., 2003; Ehrich et al., 2007; Eidesen et al., 2007a, 2007b; Hoffmann, 2012; Koch et al., 2006; Skrede et al., 2006, 2009; Westergaard et al., 2010, 2011). Particularly, species with disjunct arctic–alpine distributions have been studied in phylogeographic (reviewed by Abbott and Brochmann (2003)) and biogeographic contexts (Tkach et al., 2008c; Tolmachev, 1960; Yurtsev, 1962). The connections between the Arctic and southern high mountain ranges, such as the Alps (Ronikier et al., 2012; Schönswetter et al., 2003, 2006; Winkler et al., 2012), Rocky Mountains (Weber, 1965) or Central Asian mountains (Hedberg, 1992), are relatively well understood, to the extent that specific postglacial migration routes of the populations have been inferred (e.g., Alsos et al., 2007; Gussarova et al., 2012; Schönswetter et al., 2003, 2007). The Arctic and southern alpine regions are environmentally similar in some respects, such as having a short growing season and low mean annual temperature. But they differ in other ways. For example, frost is entirely absent in large areas of the low and middle Arctic during the growing season, whereas alpine areas experience nightly frosts during clear summer weather. Additionally, the intensity of insolation is higher in southern alpine areas, due to the steeper angle of the sun (Körner, 1995; Savile, 1972). The differences preclude a simple assumption that alpine species are necessarily pre-adapted to arctic environments.

The phylogenetic origin of the arctic flora is, however, less well known. The origins of arctic taxa have been studied in genera such as *Artemisia* (Tkach et al., 2008a, 2008b) and *Ranunculus* (Hoffmann et al., 2010), revealing, for example, ancestry in steppe or wetland habitats. In both genera, instances of *in situ* evolution of arctic taxa were also inferred, however, radiations in the Arctic were rare (Hoffmann and Röser, 2009). In *Ranunculus* some species had an alpine origin, like *R. glacialis* and *R. chamissonis* (Hoffmann et al., 2010). The alpine origin of the arctic flora has not been extensively studied in a species-level phylogenetic context despite the occurrences of frequent arctic–alpine disjunctions.

Here we concentrate on the hemiparasitic genus *Pedicularis* L. (Orobanchaceae), which includes as many as 800 described species (Mill, 2001). It is distributed primarily in colder regions throughout the northern hemisphere. The highest diversity occurs in the Hengduan Mountains of China, where about two thirds of the approximately 350 *Pedicularis* species of this area are endemic (Hong, 1983; Ree, 2005). The arctic flora includes 26–28 *Pedicularis* species, depending on the taxonomic treatment. It is thus one of the most species-rich genera in this biome, superseded only by *Carex* (92 species), *Salix* L. (67), *Potentilla* (60), *Saxifraga* (52), and *Poa* (44; Elven et al., 2011).

Most species of *Pedicularis* are hemiparasitic herbaceous perennials, some are annuals or biennials. *Pedicularis* shows a high morphological diversity particularly in flower characters, which may have co-evolved with their pollinators that are almost exclusively bumblebees collecting nectar and/or pollen (Ree, 2005 and references therein). Nevertheless, there are repeated evolutionary shifts in the shape of corolla parts that warrant further investigation with respect to their function in pollination and selective advantage (Eaton et al., 2012; Ree, 2005). In the Arctic, additionally autogamy plays a role as documented in *P. dasyantha* and *P. lapponica* (Eriksen et al., 1993; Odazs and Savolainen, 1991).

The main focus of this work was to study the origin and evolution of arctic members of *Pedicularis*. To generate a reliable phylogenetic framework we sampled all but one arctic and a high number of non-arctic species (altogether more than 200) and combined the new information with molecular phylogenetic data already published by Ree (2005). Taxon selection was further guided by the available genus-wide classifications of *Pedicularis* made on floral and vegetative characters especially by Li (1948, 1949), Vvedensky (1955) and Tsoong (1955, 1956). Morphological, caryological, ecological, and biogeographical characteristics were gathered from various literature sources to address specifically the following questions: How many times have arctic taxa evolved in the genus? What are their geographic origins? Are transitions to the Arctic associated with changes in ecological preferences, or is there evidence of niche conservatism? Is the occupation of the Arctic correlated with changes in chromosome number or traits such as plant size, flower morphology, and life form? Because many *Pedicularis* species were found in alpine regions, we hypothesized that the arctic *Pedicularis* species may be, at least partly, of high mountain origin and may have immigrated into the Arctic.

2. Materials and methods

2.1. Plant material

We sampled 218 *Pedicularis* taxa including all 25 species and 5 subspecies represented in the Arctic and listed in the Panarctic Flora (Elven et al., 2011) with exception of *P. hyperborea*, an endemic species with a small distribution range on the Yamal Peninsula of NW Siberia. Our objective was to sample the closest relatives of the arctic taxa as comprehensively as possible. Vouchers, collection localities, and ENA/GenBank DNA sequence accession numbers are listed in Table 1. *Phtheirospermum tenuisectum* (Orobanchaceae) was designated already by Ree (2005) as outgroup, *Lagotis minor* (Plantaginaceae) was chosen as another, more distantly related species.

2.2. Laboratory methods and DNA sequence analyses

Total genomic DNA was isolated from herbarium and silica gel-dried leaf material using column-based DNA extraction kits according to the protocols of the manufacturers (Macherey and Nagel, Düren, Germany, or Qiagen, Valencia, USA). PCR amplifications and direct sequencing of markers generally followed protocols used previously for *Pedicularis* (Ree, 2005). The entire internal transcribed spacer region of the nuclear ribosomal (nr) DNA (ITS1-5.8S rRNA gene-ITS2) was amplified and sequenced using the primers ITS-1, ITS-5, and ITS-4 published by White et al. (1990). Primers used for the chloroplast (cp) DNA *mat*K–*trn*K region (*mat*K gene with flanking regions of the *trn*K intron) are listed in Table 2, the primer positions are shown in Fig. 2.

Sequencing runs were carried out on an ABI automated sequencer (Applied Biosystems, Foster City, California, USA) or were performed by a commercial lab (LGC Genomics GmbH, Berlin, Germany). Sequences were automatically aligned by the program ClustalW2 (Larkin et al., 2007) and afterwards manually adjusted with the program Sequencher 5.0 (Gene Codes Corporation, Ann Arbor, MI, USA). Indels were coded as binary characters according to the simple coding algorithm of Simmons and Ochoterena (2000) using the program SeqState (Müller, 2005).

The sequence data sets were analyzed with the following methods. Maximum parsimony (MP) analysis (200 bootstrap replicates, closest taxon addition, TBR, multrees on, 1000 maxtrees) was done using the program PAUP*b10 (Swofford, 2002). Bayesian inference was performed with MrBayes version 3.1.2 (Huelsenbeck and Ronquist, 2006) and maximum likelihood (ML) analysis with RAxML version 7.2.8 under the default settings (Stamatakis, 2006) on the CIPRES Science Gateway (Miller et al., 2010). The best-fit substitution model was GTR + I + G for all data sets as determined with the hLRT implemented in MrModeltest 2.3 (Nylander, 2004). Settings for the Bayesian analysis were: nst = 6, rates = invgamma, ngen = 5,000,000, nchains = 4, temp = 0.5, samplefreq = 500. Consensus tree was computed with the first 15% discarded as burnin.

The tree topologies obtained from the separate analyses of the chloroplast and nuclear markers were examined visually for incongruence. The incongruence length difference test (Farris et al., 1995) was not used in this study to assess incongruity between the separate data sets, because the results of this overly sensitive test have repeatedly been shown to be misleading (Baker et al., 2011; Schneider et al., 2009, and references therein). We used a conservative bootstrap support (BS) of more than 85% (Baker et al., 2011; Wiens, 1998) as threshold for identification of significant incongruent positions. Due to only a weak conflict between both data sets, they were combined in a concatenated data matrix that was analyzed additionally.

2.3. Taxonomy and non-molecular data

The molecular phylogenetic tree provided the source for an evaluation of previous classifications. The tree obtained from the combined data set was compared with the taxonomical treatments of Li (1948, 1949), Vvedensky (1955), and Tsoong (1955, 1956). The clade numbering of the previously published molecular phylogeny (Ree, 2005) was continued.

Data on geographic ranges, life form, and chromosome numbers were collected for all taxa of our analysis. For the lineages including arctic taxa, additional data were collected on morphology as well as ecological preferences for habitat and soil moisture.

2.3.1. Geographic ranges

These were recorded as the presence or absence of a species in defined areas of floristic works that were used (Figs. 1 and 3), such as countries (e.g., China), continents (e.g., North America), biogeographical regions (e.g., Siberia), and high mountain ranges (e.g., Himalayas, Caucasus). The ranges were inferred from the following sources: North America (Aiken et al., 2007; Cronquist, 1959; Hultén, 1968; Vorobik, 2012), Europe (Mayer, 1972), Asia (Ivanina, 1980, 1991; Kuminova, 1960; Ohwi, 1965; Pospelova and Pospelov, 2007; Vvedensky, 1955; Vydrina, 1996; Yamazaki, 1988; Yang et al., 1998; Yurtsev et al., 2010). The distribution data were supplemented for most of the arctic species by the maps of Hultén and Fries (1986), Hultén (1968), and Meusel et al. (1978).

2.3.2. Ecological preferences

The same sources of information were used to infer the ecological preferences of the species with respect to soil moisture and altitudinal distribution. Because of the high heterogeneity of ecological categories used in the floristic literature, a broad categorization into wet, mesic, or dry habitat types was necessary (Table 3). The altitudinal distribution was also recorded as a categorical variable: alpine (above tree line), montane (frequently in mountains but not in the alpine belt), and lowlands.

2.3.3. Life form, morphology and chromosome numbers

We collected morphological characters that were available for all species across the genus' range and might have importance for growth in the Arctic (above-mentioned sources and Yamazaki, 2003a, 2003b). We recorded for all species their life form (annual, biennial, perennial). For the species of arctic lineages we collected additional data on plant height (continuous values: minimum and maximum), indumentum of the stem (categorial trait with three states: glabrous, long and densely hairy, intermediate), flower color (categorial trait with three states: yellow or white, red, both, i.e. the species may have one main color and distinct spots or section of the other color, or a species has either yellow or red flowers, e.g., *P. canadensis*), and corolla size (continuous values: minimum and maximum). The mid-range value of the continuous character measures might correspond to the mean or median values. The minimum values of plant height indicate how small a plant may become under unfavorable conditions, which need not necessarily be located in the Arctic.

Chromosome numbers were gathered from the Index to Plant Chromosome Numbers database (Goldblatt and Johnson, 1979–forthcoming) and from the floristic literature cited above.

2.4. Analysis of the lineages comprising arctic taxa

For sister-group analysis we used a set of arctic lineages, consisting of at least one arctic species and their closest non-arctic relatives that form well-supported monophyletic groups. The ecological preferences and altitudinal distribution of the species were screened for differences between arctic and non-arctic

Table 1
Taxa studied, collection information, and ENA/GenBank accession numbers. Sequences taken from GenBank are listed with the corresponding publication. Taxa represented in the Arctic are marked by an asterisk.

Taxon	Provenance, collection details, voucher information, or reference	Accession number ITS	Accession number *mat*K–*trn*K
Pedicularis abrotanifolia M.Bieb. ex Steven	Russia, 07.08.2003, S. Smirnov, A. Tribsch, F. Essl (W-2004-03642)	HG424062	HG423880
P. adunca M. Bieb. ex Steven*	Russia, Kamchatka, 17.08.1977, V.M. Starenko, I.G. Ivanova, C.S. Chumbalov (LE)	HG424063	HG423881
P. alaschanica Maxim.	China, Xizang (Tibet), 23.07.2000, D.E. Boufford et al. 29632 (A)	HG424064	HG423882
P. alatauica Stadlm. ex Vved.	Kazakhstan, Zayliyskiy Alatau, 28.05.1953, V.P. Goloskov (LE)	HG424065	HG423883
P. albertii Regel	Kyrgyzstan, Teskey Alatau, 21.05.1987, R. Aydarova (FRU)	HG424066	HG423884
P. alopecuroides Steven ex Spreng.*	Russia, Bolshoy Begichev Island, 23.08.1973, N.V. Matveeva 1142 (LE)	HG424067	HG423885
P. alopecuros Franch. ex Maxim.	China, Sichuan, 12.07.2005, D.E. Boufford et al. 32833 (A)	HG424068	HG423886
P. altaica Stephan ex Steven	Mongolia, Dzungarian Gobi Desert, 18.07.1982, E. Jäger (HAL0057321)	HG424069	HG423887
P. amoena Adams ex Steven*	Russia, Altai, 27.07.2007, S. Smirnov, A. Tribsch 9501 (SZU)	HG424070	HG423888
P. amoeniflora Vved.	Tajikistan, W Pamir, 25.06.1935, P.N. Ovczinnikov & K.S. Afanassyev 705 (LE)	HG424071	HG423889
P. anas Maxim.	China, Qinghai, 09.08.2007, D.E. Boufford et al. 39311 (A)	HG424072	HG423890
P. angustifolia Benth.	Mexico, State of Durango, 28.08.1934, F.W. Pennell 18333 (LE)	HG424073	HG423891
P. angustiloba Tsoong	China, Sichuan, 18.09.2006, D.E. Boufford et al. 36790 (A)	HG424074	HG423892
P. arguteserrata Vved.	Russia, Sayan Mts., 14.08.1962, L. Malyshev 827 (LE)	HG424075	HG423893
P. armata Maxim.	China, Qinghai, 09.08.2007, D.E. Boufford et al. 39310 (A)	HG424076	HG423894
P. armena Boiss. et Huet	Armenia, Gegharkunik, 07.06.2004, G. Fayvush et al. (W-2006–04967)	HG424077	HG423895
P. artselaeri Maxim.	China, Hopei, Nai-chiu-hsien, 14.05.1951, H.-Y. Liu 159 (LE)	HG424078	HG423896
P. ascendens Schleich. ex Gaudin	Switzerland, Valais, 15.07.2009, S. Eggenberg PA3 (Z000086355)	HG424079	HG423897
P. aspleniifolia Willd.	Austria, Salzburg, 16.08.2009, A. Tribsch 111781 (SZU)	HG424080	HG423898
P. atropurpurea Nordm.	Georgia, Racha, 15.08.2009, G. Tedoradze, D. Khuskivadze (Z000086368)	HG424081	HG423899
P. attollens A. Gray	USA, California, 25.08.2009, G.D. Barbe, T.C. Fuller (W-2006–16238)	HG424082	HG423900
P. axillaris Franch. ex Maxim.	China, Sichuan, 10.07.2004, D.E. Boufford et al. (A)	HG424083	HG423901
P. batangensis Bureau et Franch.	China, Sichuan, 10.08.2006, D.E. Boufford et al. (A)	HG424084	HG423902
P. bella subsp. *holophylla* (Marquand et Shaw) Tsoong	Ree (2005)	AY949693	AY949757
P. bifida (Buch.-Ham.) Pennell	Ree (2005)	AY949685	AY949750
P. brachystachys Bunge	Russia, Sayan Mts., 21.08.1966, I. Krasnoborov & V. Osadchiy 9631 (LE)	HG424085	HG423903
P. bracteosa Benth. var. *canbyi* (A. Gray) Cronquist	USA, Montana, Missoula, 18.07.1955, A. Cronquist 7950 (LE)	HG424086	HG423904
P. bracteosa Benth. var. *latifolia* (Pennell) Cronquist	USA, Washington, Kittitas, 14.08.1962, A.R. Kruckeberg 5525 (LE)	HG424087	HG423905
P. bracteosa Benth. var. *paysoniana* (Pennell) Cronquist	USA, Colorado, Boulder, 19.07.1965, P.J. Salamun 2121 (LE)	HG424088	HG423906
P. bracteosa Benth. var. *siifolia* (Rydb.) Cronquist	USA, Idaho, Sawtooth Mts., 09.07.1937, J.W. Thompson 13785 (LE)	HG424089	HG423907
P. brevilabris Franch.	China, Xizang (Tibet), 12.08.2004, D.E. Boufford et al. (A)	HG424090	HG423908
P. canadensis L.	Canada, Manitoba, Kleefeld, 25.05.1958, B. Boivin 11442, J.-P. Bernard, J.-M. Perron (LE)	HG424091	HG423909
P. capitata Adams*	USA, Alaska, 15.07.2009, M.K. Raynolds (Z000086357)	HG424092	HG423910
P. caucasica M. Bieb.	Georgia, Racha, 13.08.2009, G. Tedoradze, D. Khuskivadze (Z000086358)	HG424093	
	Georgia, 18.07.2002, G. Schneeweiss et al. GS/AT/MS/PS 8356 (WU4783)		HG423911
P. cephalantha Franch. ex Maxim.	China, Yunnan, 26.07.2006, D.E. Boufford et al. (A)	HG424094	HG423912
P. chamissonis Steven	Ree (2005)	AY949631	AY949709
P. cheilanthifolia Schrenk	Ree (2005)	AY949637	AY949714
P. chenocephala Diels	China, 02.08.1993, T.N. Ho et al. (A)	HG424095	HG423913
P. cinerascens Franch.	China, Sichuan, 09.07.2005, D.E. Boufford et al. (A)	HG424096	HG423914
P. comosa L.	Italy, 01.07.2007, A. Tribsch 111733 (SZU)	HG424097	HG423915
P. compacta Stephan ex Willd.*	Russia, Altai, 31.07.2008, L. Martins 2321 (B)	HG424098	
	Russia, Altai, 30.07.2002, M. Staudinger (W-2003–13325)		HG423916
P. confertiflora Prain	China, Sichuan, 07.08.2006, D.E. Boufford et al. (A)	HG424099	HG423917
P. contorta Benth.	USA, Montana, 21.08.2009, M. Apple (F)	HG424100	
	USA, Washington, 13.09.1996, A. Colwell 96, J. Meyers (WTU)		HG423918
P. cranolopha Maxim.	China, Sichuan, 16.07.1998, D.E. Boufford et al. (A)	HG424101	HG423919
P. crassirostris Bunge	Georgia, Bakuriani, 03.07.2009, G. Tedoradze, D. Khuskivadze (Z000086359)	HG424102	HG423920
P. crenulata Benth.	USA, Wyoming, Albany County, 10.07.1938, A.A. Beetle, R.M. Muir 2 (LE)	HG424103	HG423921
P. cristatella Pennell et H.L. Li	Ree (2005)	AY949638	AY949715
P. cyathophylla Franch.	China, Sichuan, 04.08.2006, D.E. Boufford et al. (A)	HG424104	HG423922
P. cyathophylloides H. Limpr.	China, Xizang (Tibet), 02.08.2004, D.E. Boufford et al. (A)	HG424105	HG423923
P. cystopteridifolia Rydb.	USA, Montana, Carbon, 25.07.1955, A. Cronquist 7974 (LE)	HG424106	HG423924
P. dasyantha (Trautv.) Hadač*	Russia, Taymyr, 30.06.1948, B.A. Tikhomirov, M.I. Vellikainen (LE)	HG424107	HG423925

P. dasystachys Schrenk (1)	Russia, Khakassiya, 17.06.1970, I. Neufeld, R. Kharitonova (LE)	HG424108	HG423926
P. dasystachys Schrenk (2)	Russia, Kurganskaya obl., 15.06.2000, L.V. Mamontova (LE)	HG424109	HG423927
P. davidii Franch.	China, Sichuan, 20.08.2007, D.E. Boufford et al. (A)	HG424110	HG423928
P. debilis Franch. ex Maxim.	Yang et al. (2003)	AY155293	
	China, Sichuan, 19.07.2004, D.E. Boufford et al. (A)		HG423929
P. decorissima Diels	China, Sichuan, 05.08.2005, D.E. Boufford et al. (A)	HG424111	HG423930
P. densiflora Benth.	USA, California, San Mateo County, 24.02.1935, L.S. Rose 35016 (LE)	HG424112	HG423931
P. densispica Franch. ex Maxim.	Ree (2005)	AY949642	AY949718
P. dichotoma Bonati	China, Sichuan, 22.07.1998, D.E. Boufford et al. (A)	HG424113	HG423932
P. dolichocymba Hand.-Mazz.	Ree (2005)	AY949633	AY949711
P. dolichoglossa H.L. Li	Ree (2005)	AY949639	AY949716
P. dolichorrhiza Schrenk	Afghanistan, Prov. Bamian, 27.06.1962, I. Hedge & P. Wendeblo 4667 (LE)	HG424114	HG423933
P. dubia B. Fedtsch.	Kyrgyzstan, Turkestanskiy ridge, 15.06.2006, M.R. Tanybaeva (LE)	HG424115	HG423934
P. elongata A. Kern.	Italy, Trentino, Alto Adige, 10.07.2009, B. Fischer (Z)	HG424116	HG423935
P. elwesii Hook. f.	Ree (2005)	AY949649	AY949723
P. eriantha (Boiss. et Buhse) T.N. Popova	Georgia, Bakuriani, 03.07.2009, G. Tedoradze, D. Khuskivadze (Z000086360)	HG424117	HG423936
P. eriophora Turcz.*	Russia, Kamchatka, 08.07.1960, I.G. Ivanova (LE)	HG424118	HG423937
P. fetisowii Regel	China, Xizang (Tibet), 23.07.2000, D.E. Boufford et al. (A)	HG424119	HG423938
P. fissa Turcz.	Russia, E Sayan Mts., 17.08.1961, L. Malyshev 1091 (LE)	HG424120	HG423939
P. flammea L.*	Greenland, Disco, Qasigissat, Vesterdalen, 17.08.1982, M. Sasa 2066 (LE)	HG424121	HG423940
P. flava Pall.	Mongolia, Ulan-Bator, 17.06.1982, E. Jäger (HAL0058124)	HG424122	HG423941
P. flexosoides T. Yamaz.	Bhutan, Gasa Distr., 26.07.2000, G. & S. Miehe (TI)	HG424124	HG423943
P. foliosa L.	Ree (2005)	AY949679	AY949745
P. fragarioides Tsoong	China, Sichuan, 09.07.2005, D.E. Boufford et al. (A)	HG424125	HG423944
P. furfuracea Wall. ex Benth.	Ree (2005)	AY949701	AY949765
P. geosiphon Harry Sm. et Tsoong	China, Sichuan, 21.07.2005, D.E. Boufford et al. (A)	HG424126	HG423945
P. glabrescens H. L. Li	China, Sichuan, 12.07.1998, D.E. Boufford et al. (A)	HG424127	HG423946
P. gloriosa Bisset et S. Moore	Ree (2005), Fujii (2007)	AY949647	AB280522
P. grandiflora Fisch.	Russia, S Yakutia, 24.07.1991, O.A. Zolotovskiy (LE)	HG424128	HG423947
P. grayi A. Nelson	USA, Colorado, Gunnison, 13.07.1960, C. Chaney (LE)	HG424129	HG423948
P. groenlandica Retz.*	USA, Montana, Carbon, 02.08.1955, A. Cronquist 8043 (LE)	HG424130	HG423949
P. gyroflexa Vill.	Italy, 28.06.2009, A. Tribsch 111674 (SZU)	HG424131	HG423950
P. hirsuta L.*	Greenland, Qaasuitsup, Aasiat, 08.07.2006, K. Westergaard AK1151 (O)	HG424132	HG423951
P. incarnata L.	Russia, Altai, 21.07.2000, S. Leffler S15 (HAL)	HG424133	HG423952
P. inconspicua Vved.	Uzbekistan, Kugitang ridge, 05.06.1982, R.V. Kamelin et al. 836 (LE)	HG424134	HG423953
P. ingens Maxim.	China, Sichuan, 03.09.1997, D.E. Boufford et al. (A)	HG424135	HG423954
P. integrifolia Hook. f.	China, Sichuan, 06.08.2007, D.E. Boufford et al. (A)	HG424136	HG423955
P. interrupta Stephan	Russia, Altai, 24.07.2000, S. Leffler S17 (HAL)	HG424137	HG423956
P. iwatensis Ohwi ITS	Ree (2005), Fujii (2007)	AY949654	AB280513
P. julica E. Mayer	Slovenia, Gorenjska, 01.07.2009, B. Frajman (Z000086363)	HG424138	HG423957
P. kansuensis Maxim.	China, Sichuan, 29.08.1997, D.E. Boufford et al. (A)	HG424139	HG423959
P. karatavica Pavlov	Kyrgyzstan, Ichkeletau Mts., 12.06.1974, R.V. Kamelin 1289 (LE)	HG424140	HG423960
P. keiskei Franch. et Sav.	Japan, s.d., N. Fujii (KUMA)	HG424141	HG423961
P. kerneri Dalla Torre	Switzerland, s.d., R. Nyeffler (A)	HG424142	HG423962
P. korolkowii Regel	Kyrgyzstan, W Tian-Shan, 11.08.1966, I.A. Gubanov 186 (LE)	HG424143	HG423963
P. krylovii Bonati	Uzbekistan, W Hissar Mts., 13.06.1982, R.V. Kamelin et al. 1156 (LE)	HG424144	HG423964
P. kusnetzovii Kom.	Russia, Far East, 25.07.2005, V.M. Van 76485/3 (LE)	HG424145	HG423965
P. labradorica Wirsing*	Russia, Taymyr, 17.07.1982, Y.P. Kozhevnikov (LE)	HG424146	HG423966
P. lachnoglossa Hook. f.	Ree (2005)	AY949658	AY949728
P. lanata Willd. ex Cham. et Schltdl. (1)*	Russia, Chukotka, 04.07.1980, A.A. Korobkov, N.A. Sekretareva (LE)	HG424147	HG423967
P. lanata Willd. ex Cham. et Schltdl. (2)*	USA, Alaska, 19.07.2009, M.K. Raynolds (Z000086364)	HG424148	HG423958
P. lanceolata Michx.	Canada, Rainy River District, 20.08.1961, C.E. Garton 9486 (LE)	HG424149	HG423968
P. langsdorffii Fisch. ex Steven*	Russia, Chukotka, 10.07.1980, A.A. Korobkov, N.A. Sekretareva (LE)	HG424150	HG423969
P. lapponica L.*	Russia, Chukotka, 01.07.1980, A.A. Korobkov, N.A. Sekretareva (LE)	HG424151	HG423970
P. lasiophrys Maxim.	Ree (2005)	AY949662	AY949732
P. lasiostachys Bunge	Mongolia, Prov. Archangaj, 05.07.1978, H.D. Knapp (HAL0056788)	HG424152	HG423971
P. latituba Bonati	China, Xizang (Tibet), 04.08.2004, D.E. Boufford et al. (A)	HG424153	HG423972
P. likiangensis Franch. ex Maxim.	Ree (2005)	AY949659	AY949729
P. lineata Franch. ex Maxim.	Ree (2005)	AY949664	AY949734

(*continued on next page*)

Table 1 (*continued*)

Taxon	Provenance, collection details, voucher information, or reference	Accession number ITS	Accession number *mat*K–*trn*K
P. longiflora Rudolph	Ree (2005)	AY949645	AY949721
P. longipes Maxim.	China, Sichuan, 16.08.2007, D.E. Boufford et al. (A)	HG424154	HG423973
P. ludwigii Regel	Kyrgyzstan, Osh Province, 10.07.1987, R. Aydarova, Kashlaraeva (FRU)	HG424155	HG423974
P. lyrata Prain ex Maxim.	Ree (2005)	AY949648	AY949722
P. macrochila Vved.	Kyrgyzstan, Tian-Shan, 21.06.1958, I.A. Gubanov 203/93 (LE)	HG424156	HG423975
P. macrosiphon Franch.	China, Sichuan, 24.07.2007, D.E. Boufford et al. (A)	HG424157	HG423976
P. mariae Regel	Kazakhstan, NW Tian-Shan, Kunchey Alatau, 07.07.1952, V.P. Goloskov (LE)	HG424158	HG423977
P. maximowiczii Krasn.	Kazakhstan, Alma-Atinskaya obl., 10.07.1935, B. Schischkin (LE)	HG424159	HG423978
P. megalantha D. Don	Ree (2005)	AY949656	AY949727
P. merrilliana H.L. Li	China, Xizang (Tibet), 17.07.2000, D.E. Boufford et al. (A)	HG424160	HG423979
P. metaszetschuanica Tsoong	China, Sichuan, 16.08.2007, D.E. Boufford et al. (A)	HG424161	HG423980
P. microchila Franch. ex Maxim.	China, Sichuan, 28.07.2007, D.E. Boufford et al. (A)	HG424162	HG423981
P. mixta Gren. ex Gren. et Godr.	Spain, 10.06.2005, A. Tribsch 10702 (SZU)	HG424163	HG423982
P. mollis Wall. ex Benth.	Ree (2005)	AY949671	AY949739
P. muscoides H. L. Li	Ree (2005)	AY949635	AY949713
P. mussotii Franch.	China, Sichuan, 04.08.2006, D.E. Boufford et al. 35733 (A)	HG424164	HG423983
P. myriophylla Pall.	Mongolia, Ulan-Bator, 08.08.1976, W. Hilbig, Z. Schamsran (HAL0058303)	HG424165	HG423984
P. nasuta M. Bieb. ex Steven*	Russia, Sakhalin, 20.07.1968, T.I. Nechaeva (LE)	HG424166	HG423985
P. nipponica Makino	Ree (2005)	AY949663	AY949733
P. nodosa Pennell	China, Xizang (Tibet), 03.09.1984, G. Miehe (TI)	HG424167	
	Nepal, Dauragili Zone, 04.09.1999, K. Fujikawa (TI)		HG423986
P. oederi Vahl. *	Russia, Altai, 01.07.2009, P.E. Berry (MICH)	HG424168	
	USA, Alaska, 15.07.2009, M.K. Raynolds (Z000086369)		HG423987
P. oliveriana Prain	China, Xizang (Tibet), 14.08.2000, D.E. Boufford et al. (A)	HG424169	HG423988
P. ornithorhyncha Benth.	Canada, British Columbia, Vancouver Island, 06.08.1961, J.A. Calder 32209, K.T. MacKay (LE)	HG424170	HG423989
P. oxycarpa Franch. ex Maxim.	China, Sichuan, 21.07.2005, D.E. Boufford et al. (A)	HG424171	HG423990
P. oxyrhyncha T. Yamaz.	Ree (2005)	AY949651	AY949724
P. pallasii Vved.*	Russia, Kamchatka, 08.06.1909, E. Bezais 23 (LE)	HG424172	HG423991
P. palustris L. subsp. *opsiantha* (Ekm.) Er. Almq.*	Finnland, Etelä-Savo, Valkeala, 16.07.1960, T. Ulvinen (LE)	HG424173	HG423992
P. parryi A. Gray	USA, Wyoming, Big Horn County, 16.07.1949, F.W. & J.R. Pennell 26887 (LE)	HG424174	HG423993
P. parviflora Sm.*	USA, Alaska, 25.06.1979, M.C. Muller 3100 (LE)	HG424175	HG423994
P. pauciflora Pennell	Ree (2005)	AY949634	AY949712
P. pectinatiformis Bonati	China, Xizang (Tibet), 01.08.2004, D.E. Boufford et al. (A)	HG424176	HG423995
P. peduncularis Popov	Kyrgyzstan, Turkestanskiy ridge, 01.06.2007, M.R. Tanochbaeva (LE)	HG424177	HG423996
P. pennelliana Tsoong	Ree (2005)	AY949655	AY949726
P. pennellii Hultén*	Russia, Taymyr, 23.07.1982, Y.P. Kozhevnikov (LE)	HG424178	HG423997
P. pheulpinii Bonati	China, Qinghai, 02.08.1993, T.N. Ho et al. (A)	HG424179	HG423998
P. physocalyx Bunge	Kazakhstan, Uralskaya obl., 62.001, T.E. Darbaeva (LE)	HG424180	HG423999
P. pilostachya Maxim.	China, Xizang (Tibet), 07.08.2004, D.E. Boufford et al. (A)	HG424181	HG424000
P. pontica Boiss.	Georgia, Svaneti, 19.08.2009, G. Tedoradze, D. Khuskivadze (Z000086368)	HG424182	HG424001
P. popovii Vved.	Kyrgyzstan, Turkestanskiy ridge, 18.04.2007, M.R. Tanybaeva (FRU)	HG424183	HG424002
P. proboscidea Steven	Kazakhstan, Kalbinskiy ridge, 06.07.1965, V.I. Vassilevich et al. 2491 (LE)	HG424184	HG424003
P. procera Adams ex Steven	USA, Colorado, 26.07.1878, M.E. Jones 848 (LE)	HG424185	HG424004
P. przewalskii Maxim.	Ree (2005)	AY949677	AY949743
P. pubiflora Vved.	Central Asia, Zayliyskiy Alatau, 15.07.1936, V.P. Goloskov (LE)	HG424186	HG424005
P. pulchra Pauls.	Tajikistan, Badakhshan, 19.06.1966, R.V. Kamelin (LE)	HG424187	HG424006
P. pycnantha Boiss.	Turkmenistan, Kopet-Dag, 21.05.1963, I.A. Gubanov 357 (LE)	HG424188	HG424007
P. pyrenaica J. Gay	France, Dépt. Pyrénées-Orientales, 09.08.1997, M. Röser 10542 (HAL)	HG424189	HG424008
P. qinghaiensis T. Yamaz.	China, Qinghai, 02.08.2002, G. Miehe, Sonamco, K. Koch (TI)	HG424190	HG424009
P. racemosa Dougl. ex Hook. subsp. *alba* Pennell	USA, Montana, 14.07.1955, A. Cronquist 7925 (LE)	HG424191	HG424010
P. recurva Maxim.	China, Sichuan, 21.07.2005, D.E. Boufford et al. (A)	HG424192	HG424011
P. resupinata L.	Russia, Altai, 01.08.2008, L. Martins 2333 (B), Fujii (2007)	HG424193	AB280527
P. rex C.B. Clarke ex Maxim.	China, Sichuan, 12.07.2005, D.E. Boufford et al. (A)	HG424194	HG424012
P. rhinanthoides Schrenk ex Fisch. et C.A. Mey.	Ree (2005)	AY949691	AY949755

P. rhizomatosa Tsoong	China, Xizang (Tibet), 26.07.2000, D.E. Boufford et al. (A)	HG424195	HG424013
P. rhodotricha Maxim.	Ree (2005)	AY949674	AY949741
P. rhynchodonta Bureau et Franch.	Ree (2005)	AY949682	AY949748
P. rosea Wulf	Austria, Steiermark, 09.06.2003, A. Tribsch 8794 (SZU)		HG424014
P. rosea Wulf subsp. *allionii* (Rchb. fil.) Arcang.	Italy, Paro Distr., 28.06.2009, A. Tribsch 111687 (SZU)	HG424196	
P. roseialba T. Yamaz.	Bhutan, 10.07.2000, G. & S. Miehe (TI)	HG424197	HG424015
P. rostratocapitata Crantz	Austria, Salzburg, 16.08.2009, A. Tribsch 111785 (SZU)	HG424198	HG424016
P. roylei Maxim.	China, Sichuan, 19.07.2004, D.E. Boufford et al. (A)	HG424199	HG424017
P. rubens Stephan ex Willd.	Mongolia, Ulan-Bator, 26.06.1979, K. Helmecke (HAL0056205)	HG424200	HG424018
P. rudis Maxim.	Ree (2005)	AY949686	AY949751
P. rupicola Franch. ex Maxim.	Ree (2005)	AY949688	AY949752
P. salviiflora Franch.	China, Yunnan, 26.07.2006, D.E. Boufford et al. (A)	HG424201	HG424019
P. sceptrum-carolinum L.*	Poland, Wigry National Park, 16.08.2008, A. Wróblewska (BIL)	HG424202	HG424020
P. schistostegia Vved.	Ree (2005)	AY949704	AY949767
P. schizorrhyncha Prain	Bhutan, Thimphu Distr., 19.07.2000, G. & S. Miehe (TI)	HG424203	HG424021
P. schugnana B. Fedtsch.	Tajikistan, Pamir, Lake Sarezskoe, 08.07.1958, Y. Gusev 5189 (LE)	HG424204	HG424022
P. scolopax Maxim.	China, Xizang (Tibet), 27.07.2004, D.E. Boufford et al. (A)	HG424205	
	China, Xizang (Tibet), 20.07.2000, D.E. Boufford et al. 29558 (A)		HG424023
P. scopulorum A. Gray	USA, Colorado, 14.07.1963, G.N. Jones 36089 (LE)	HG424206	HG424024
P. scullyana Prain ex Maxim.	Nepal, 1999, K. Fujikawa 9920105 (A)	HG424207	
	Nepal, 1999, Omori et al. 9950026 (A)		HG424025
P. semenowii Regel	Kyrgyzstan, Ala-Archa, 04.05.1983, R. Aydarova, Chypaev (FRU)	HG424208	HG424026
P. semibarbata A. Gray	USA, California, 24.07.2003, A. Colwell 0325 (WTU)	HG424209	HG424027
P. sibirica Vved.	Russia, Altai, 30.05.2002, M.H. Hoffmann Mo2/67 (HAL)	HG424210	HG424028
P. sibthorpii Boiss.	Turkey, Erzurum, 15.06.2002, G. Schneeweiss, C.-G. Jang GS/CJ 7778 (WU4552)	HG424211	
	Georgia, 20.07.1997, P. Schönswetter, A. Tribsch (WU4161)		HG424029
P. siphonantha D. Don	China, Sichuan, 04.07.1998, D.E. Boufford et al. (A)	HG424212	
	China, Sichuan, 02.07.1998, D.E. Boufford et al. (A)		HG424030
P. spec.	China, Xizang (Tibet), 18.08.2000, D.E. Boufford et al. (A)	HG424123	HG423942
P. spicata Pallas	China, 06.06.2005, Liu, Quan-Ru (BNU)	HG424213	HG424031
P. steiningeri Bonati	China, Sichuan, 07.08.2006, D.E. Boufford et al. (A)	HG424214	
	China, Qinghai, 28.08.1996, Sino-American-British Yushu Expedition (1996) 2510 (E00061464)		HG424032
P. streptorhyncha Tsoong	Ree (2005)	AY949689	AY949753
P. sudetica Willd. subsp. *albolabiata* Hultén*	Russia, Chukotka, 02.08.1980, A.A. Korobkov, N.A. Sekretareva (LE)	HG424215	HG424033
P. sudetica Willd. subsp. *arctoeuropaea* Hultén*	Russia, Polar Ural, 14.07.1961, K. Igoschina (LE)	HG424216	HG424034
P. sudetica Willd. subsp. *gymnostachya* (Trautv.) Jurtzev et V.V. Petrovsky*	Russia, Yakutia, 03.07.1977, Y.P. Kozhevnikov & V.V. Ukraintseva 207 (LE)	HG424217	HG424035
P. sudetica Willd. subsp. *interioroides* Hultén*	Russia, Yamal Peninsula, 20.07.1979, O.V. Rebristaya 3146a (LE)	HG424218	HG424036
P. sudetica Willd. subsp. *interioroides* Hultén var. *villosula* Ivanina et Jurtzev*	Russia, Sibiryakov Island, 13.08.1980, N.V. Matveeva & L.L. Zanokha 2799 (LE)	HG424219	HG424037
P. sudetica Willd. subsp. *pacifica* Hultén*	Russia, Chukotka, 197#, Y.P. Kozhevnikov 31773 (LE)	HG424220	HG424038
P. superba Franch. ex Maxim.	Ree (2005)	AY949684	AY949749
P. sylvatica L.	Deutschland, Hessen, 16.05.1983, M. Röser 1043 (HAL)	HG424221	HG424039
P. szetschuanica Maxim.	China, Sichuan, 28.07.2007, D.E. Boufford et al. (A)	HG424222	HG424040
P. talassica Vved.	Kyrgyzstan, Chatkalskiy ridge, 01.06.2007, G.A. Lazkov (LE)	HG424223	HG424041
P. tatsienensis Bureau et Franch.	Ree (2005)	AY949660	AY949730
P. ternata Maxim.	Ree (2005)	AY949694	AY949758
P. thamnophila (Hand.-Mazz.) H.L. Li	China, Yunnan, 25.07.2006, D.E. Boufford et al. (A)	HG424224	HG424042
P. tianschanica Rupr.	Kyrgyzstan, Alay ridge, 18.07.1930, S.V. Yuzepszuk 585 (LE)	HG424225	HG424043
P. tibetica Franch.	Ree (2005)	AY949644	AY949720
P. tongolensis Franch.	China, Xizang (Tibet), 11.08.2000, D.E. Boufford et al. (A)	HG424226	HG424044
P. torta Maxim.	China, Sichuan, 30.07.2007, D.E. Boufford et al. (A)	HG424227	HG424045
P. trichocymba H.L. Li	China, Xizang (Tibet), 23.07.2000, D.E. Boufford et al. (A)	HG424228	
	China, Sichuan, 04.07.1998, D.E. Boufford et al. (A)		HG424046
P. trichoglossa Hook. f.	China, Xizang (Tibet), 03.08.2004, D.E. Boufford et al. (A)	HG424229	HG424047
P. tricolor Hand.-Mazz.	China, Sichuan, 06.08.2005, D.E. Boufford et al. (A)	HG424230	HG424048
P. tristis L.*	Russia, 37.07.2003, S. Smirnov, A. Tribsch 9541 (SZU)	HG424231	HG424049
P. tuberosa L.	Austria, Tirol, 20.07.2007, P. Pilsl 17602 (SZU)	HG424232	HG424050

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Table 1 (*continued*)

Taxon	Provenance, collection details, voucher information, or reference	Accession number ITS	Accession number *matK*–*trnK*
P. uliginosa Bunge	Russia, Altai, 25.07.2000, M.H. Hoffmann M94 (HAL)	HG424233	HG424051
P. uralensis Vved.	Russia, Bashkiriya, 19.06.1974, K. Werner (HAL0043149)	HG424234	HG424052
P. urceolata Tsoong	China, Sichuan, 07.08.2006, D.E. Boufford et al. (A)	HG424235	HG424053
P. venusta Schangin ex Bunge	Mongolia, Changai, 27.06.1983, W. Hilbig (HAL0050499)	HG424236	HG424054
P. verticillata L. (1)*	Russia, Altai, 21.07.2000, S. Leffler S10 (HAL)	HG424237	HG424055
P. verticillata L. (2) *	Ree (2005)	AY949698	AY949762
P. villosa Ledeb. ex Spreng. (1)*	Russia, Chukotka, 24.07.1980, A.A. Korobkov, N.A. Sekretareva (LE)	HG424238	HG424056
P. villosa Ledeb. ex Spreng. (2)*	Russia, Taymyr, Byrranga Mts., 30.07.1980, Y.P. Kozhevnikov 163 (LE)	HG424239	HG424057
P. violascens Schrenk ex Fisch. et C.A. Mey.	Kyrgyzstan, 17.08.1998, G. Lazkov (FRU)	HG424240	HG424058
P. waldheimii Bonati	C Asia, Pamir-Alay, 16.07.1962, V.P. Botschantzev 167 (LE)	HG424241	HG424059
P. wilhelmsiana Fisch. ex M. Bieb.	Georgia, Bakuriani, 03.07.2009, G. Tedoradze, D. Khuskivadze (Z000086371)	HG424242	HG424060
P. yezoensis Maxim.	Ree (2005), Fujii (2007)	AY949683	AB280531
Outgroups			
Phtheirospermum tenuisectum Bureau et Franch.	Ree (2005)	AY949708	AY949770
Lagotis minor (Willd.) Standl.	Russia, W Taymyr, 03.08.1981, N.V. Matveeva & L.L. Zanokha 3224 (LE)	HG424243	HG424061

Table 2
Primers used for sequencing of the chloroplast *mat*K–*trn*K DNA region.

Primer name	Primer sequence	Reference
Ped-*trn*K5	GTGCGGCTAGAATCTTTTAC	This study
*trn*K11	CTCAACGGTAGAGTACTCG	Young et al. (1999)
*mat*K510r	GAAGAGTTTGAACCAAKAYTTCC	Young et al. (1999)
*trn*K710F	GTATCGCACTATGTWTCATTTGA	Paun et al. (2005)
*trn*K685F	GTATCGCACTATGTATCATTTGA	M. Wojciechowski (pers. comm.)
3F-KIM	CGTACAGTACTTTTGTGTTTACGAG	Yu et al. (2011)
Ped-*mat*K1570F	CTRTGGTTGGTCAAGGAA	This study
*trn*K2R*	CCCGGAACTAGTCGGATGG	M. Wojciechowski (pers. comm.)

species. A meaningful ancestral character state reconstruction for the arctic species was hampered by the sometimes low resolution of the phylogenetic tree, particularly at the terminal clades. Because of this lack of resolution, we focused instead on character states that differentiate the arctic species from their non-arctic relatives and are possibly linked with the occupation of arctic environments.

Continuous morphological data were analyzed using the Wilcoxon range tests. Categorial morphological data were analyzed with the Fishers exact test. Calculations were done with the statistical package R (R Core Team, 2012).

3. Results

3.1. Nuclear, chloroplast, and combined DNA data sets

The nrDNA ITS and 5.8S gene sequences ranged between 673 and 700 base pairs (bp). The alignment matrix consisted of 736 bp with an average divergence between sequences of 7.4%. We counted 423 (58.2%) variable with 316 (74.7%) parsimony-informative positions. This high sequence divergence of the ITS is in accordance to observations of Yang et al. (2003).

The sequences of the *mat*K gene including flanking parts of the *trn*K intron were between 2350 and 2450 bp long. The alignment comprised 2676 nucleotide positions, the sequence divergence amounted to 2.4%. A total of 981 (37.2%) characters were variable and 485 (49.4%) of them were parsimony-informative.

The alignment was straightforward for both genome markers and no nucleotide position was excluded from the analyses. The resolution of the phylogenetic trees calculated separately for the nuclear and chloroplast marker, respectively, was rather low (Supplemental information). We observed only *P. villosa* and *P. dasystachys* to switch between sister clades. In the ITS tree *P. villosa* formed together with *P. schistostegia* a clade with 86% BS support, the taxa of the *P. sudetica* group and *P. dasystachys* were in a clade with 88% BS support. In the *mat*K tree *P. schistostegia* clustered with *P. flava* (93% BS support), the other mentioned taxa were not resolved at the 85% threshold. These small differences may not preclude a combination of the nuclear and chloroplast data sets.

The phylogenetic resolution was improved by using the combined data set. Maximum parsimony (MP) analysis yielded 10,000 shortest trees with 4848 steps, a consistency index (CI) of 0.419, and a retention index (RI) of 0.698. The strict consensus tree shown in Fig. 3 was congruent with the maximum likelihood (ML; $-\ln L = 35{,}926.35$ for the best model) and the Bayesian trees (not shown). The backbone of the phylogenetic tree has only weakly supported branches.

3.2. Phylogeny of Pedicularis: Sections and series revealed to be mainly para- or polyphyletic

The phylogeny of *Pedicularis* of the combined nuclear and chloroplast data set is given in Fig. 3. This reveals eight major

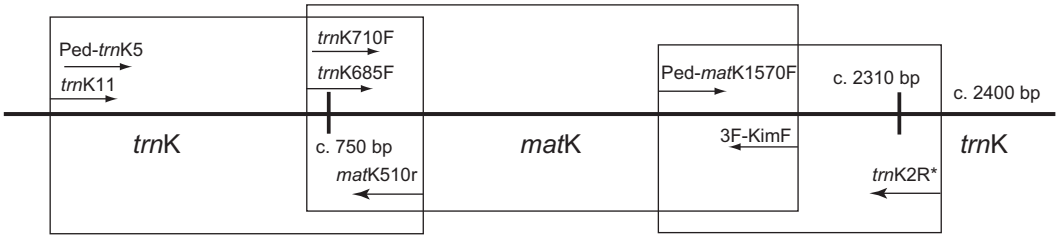

Fig. 2. Position and sequencing direction of the *mat*K–*trn*K primers used.

clades labeled 1–8 that were addressed in ascending order as they appear in the tree (cf. Section 2). Support values are specified in the following as ML BS/Bayesian posterior probability/MP BS.

3.2.1. Clade 6

The species of this clade (97/1.00/89) are distributed mostly in North America and/or East Asia. *Pedicularis sceptrum-carolinum* and *P. capitata* are widespread in the Palaearctic. The monophyletic section *Gloriosae* (92/1.00/57) with three endemics of Japan and *P. sceptrum-carolinum* is sister to a clade (100/1.00/100) composed of the North American species from series *Brevilabres*, *Capitatae*, and *Lunares*. *Pedicularis recurva* from China (series *Recurvae*) clustered with three species from North America that were considered to be only distantly related (Tsoong, 1956). *Pedicularis cystopteridifolia* was treated as a member of series *Sudeticae* (Tsoong, 1956), whose other species belong to Clade 8.

3.2.2. Clade 5

In this clade (76/1.00/57) the monophyletic series *Lasiophrydes* (two species, China) and *Trichoglossae* (two species, Himalayas to China) were placed along with the five sampled species of series *Craspedotrichae* (14 species, Himalayas and China) and the monotypic series *Dolichocymbae* (China), *Rudes* (six species, China to N Myanmar), and *Tristes* (three species, Siberian Arctic to China).

3.2.3. Clades 2–4, 7

Species of these clades are generally distributed in China and the Himalayas (Fig. 3), with only few species distributed more widely in Asia (e.g., *P. longiflora*), Europe and North America (e.g., *P. flammea*, *P. oederi*). Clade 2 (87/1.00/74) included the sampled species of the small series *Megalanthae*, a group of about five species (Ree, 2005; Yang et al., 1998).

3.2.4. Clade 7

This clade (73/1.00/50) contained annual and perennial species mostly distributed in the high mountains of the Himalayas and China. Two species have other distribution patterns, *P. oederi* occupies a wide circumpolar range, *P. flammea* occurs only in Greenland and Eastern North America. This clade comprised the species of ser. *Flammeae* as well as four recently described species (Yamazaki, 2003a, 2003b). *Pedicularis bella* and *P. rhynchodonta* were affiliated with the polyphyletic sect. *Rhizophyllum* (Li, 1949).

3.2.5. Clade 3

(100/1.00/100) comprised four paraphyletic series: *Longiflorae* (21 species in Asia), *Oxycarpae* (nine species, China), *Franchetianae* (two species, China), *Oliganthae* (seven species, China) and the paraphyletic sections *Carnosae* (twelve species, eastern Asia) and *Pseudomacranthae* (four species, eastern Asia). Clade 4 (96/1.00/96) encompasses species traditionally ascribed to many different series (*Reges*, *Cyathophylloides*, *Cyathophyllae*, *Superbae, Macranthae*, *Pumiliones*) distributed mostly in China and with a few species in the Himalayas.

3.2.6. Clade 1

This clade (98/1.00/96) contained 63 species from at least 17 different series and sections of the monograph of *Pedicularis* for China (Li, 1948, 1949), the worldwide classification of the genus by Tsoong (1955, 1956), the Flora SSSR (Vvedensky, 1955), and the recent Flora of China treatment (Yang et al., 1998). It comprised species from the comparatively large sections *Verticillatae* (c. 37 species in Eurasia and NW North America) and *Debiles* (15 species in the Himalayas and China). Other species in this clade were from series *Myriophyllae* (nine species distributed in Siberia, eastern Asia, and Alaska), section *Abrotanifoliae* (six species in Central to eastern mainland Asia) as well as from similar-sized or even smaller (*Amoenae*, *Caucasicae*, *Pycnanthae*, *Semenovianae*) or monotypic series (e.g., *Dichotomae*, *Integrifoliae*, China and the Himalayas). The larger sections and series were para- or polyphyletic according to our phylogenetic tree.

3.2.7. Clade 8

This large clade (92/1.00/80) of 76 taxa was represented by only six species in the previous study of Ree (2005: Fig. 3, between clades 1 and 2). The clade includes taxa of at least 18 series recognized by Li (1948, 1949), Tsoong (1955, 1956, 1963), and Yang et al. (1998) as well as additional species that were not assigned to any series by these treatments. Many of the latter were treated by Vvedensky (1955) in the account for the Flora SSSR, which, conversely, did not deal with the species outside of the former Soviet Union and followed a different taxonomic concept.

Clade 8 comprised the large series *Comosae* and *Dolichorrhizae* (altogether c. 30 species, Eurasia), *Rostratae* (c. 17 species, Europe and outposts in Asia Minor), *Racemosae*, *Compactae* (altogether c. 11 species, Holarctic), and *Pedicularis* (12 species, worldwide). None of these series was monophyletic. Even some of the smaller series like *Surrectae* (three species, North America, Greenland) and *Foliosae* (seven species, Europe to Siberia) were paraphyletic. The series *Sudeticae* incl. *Elatae* (nine species, Holarctic) was highly polyphyletic, because *P. cystopteridifolia* occured in Clade 6 and the other species in Clade 8. Some branches within Clade 8 received considerable support, but were not defined by striking morphological, ecological or other characteristics.

3.3. Lineages comprising arctic Pedicularis

The arctic species of *Pedicularis* occur in 13 lineages of varying size that are dispersed across the molecular phylogeny (Fig. 3). This suggests that arctic *Pedicularis* originated at least 12 times, if arctic clades in polytomies were not counted as independent. If all arctic lineages evolved independently, the arctic taxa evolved as many as 14 times.

3.3.1. Pedicularis sceptrum-carolinum lineage

This branch of *Pedicularis* is part of the early diverging Clade 1 and comprised a branch with North American species and one with species from eastern Asia (Japan, Russian Far East, Korea, China).

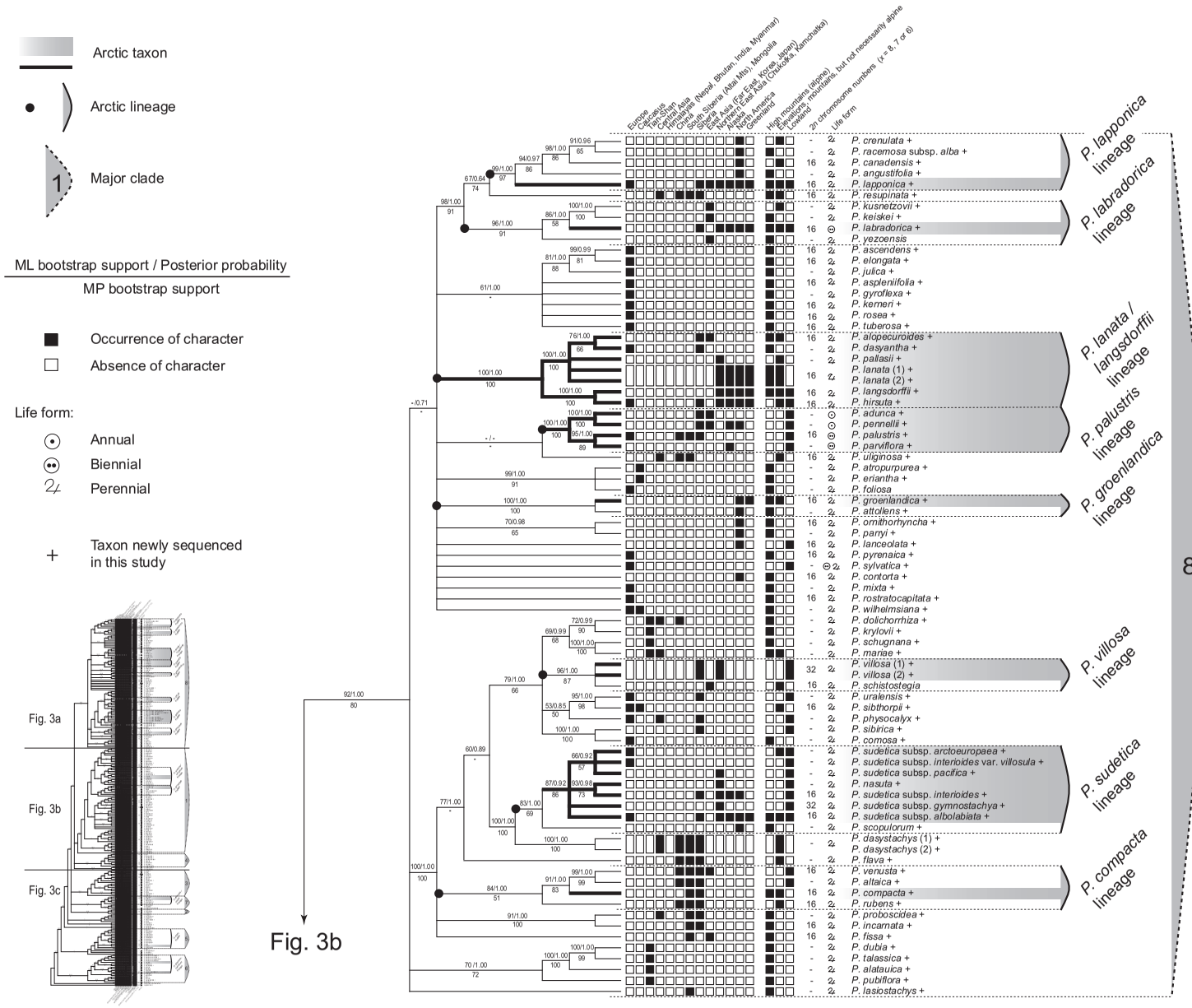

Fig. 3. Strict consensus tree from parsimony analysis of the combined nr ITS and cp *matK* data set. Values above the branches indicate maximum likelihood bootstrap percentage ⩾50 and Bayesian posterior probability ⩾0.50, the value below the branches means maximum parsimony bootstrap percentage ⩾50. Major clade numbering (clades 1–6) follows Ree (2005), clades 7 and 8 were newly observed. The clades were described in the text in ascending order.

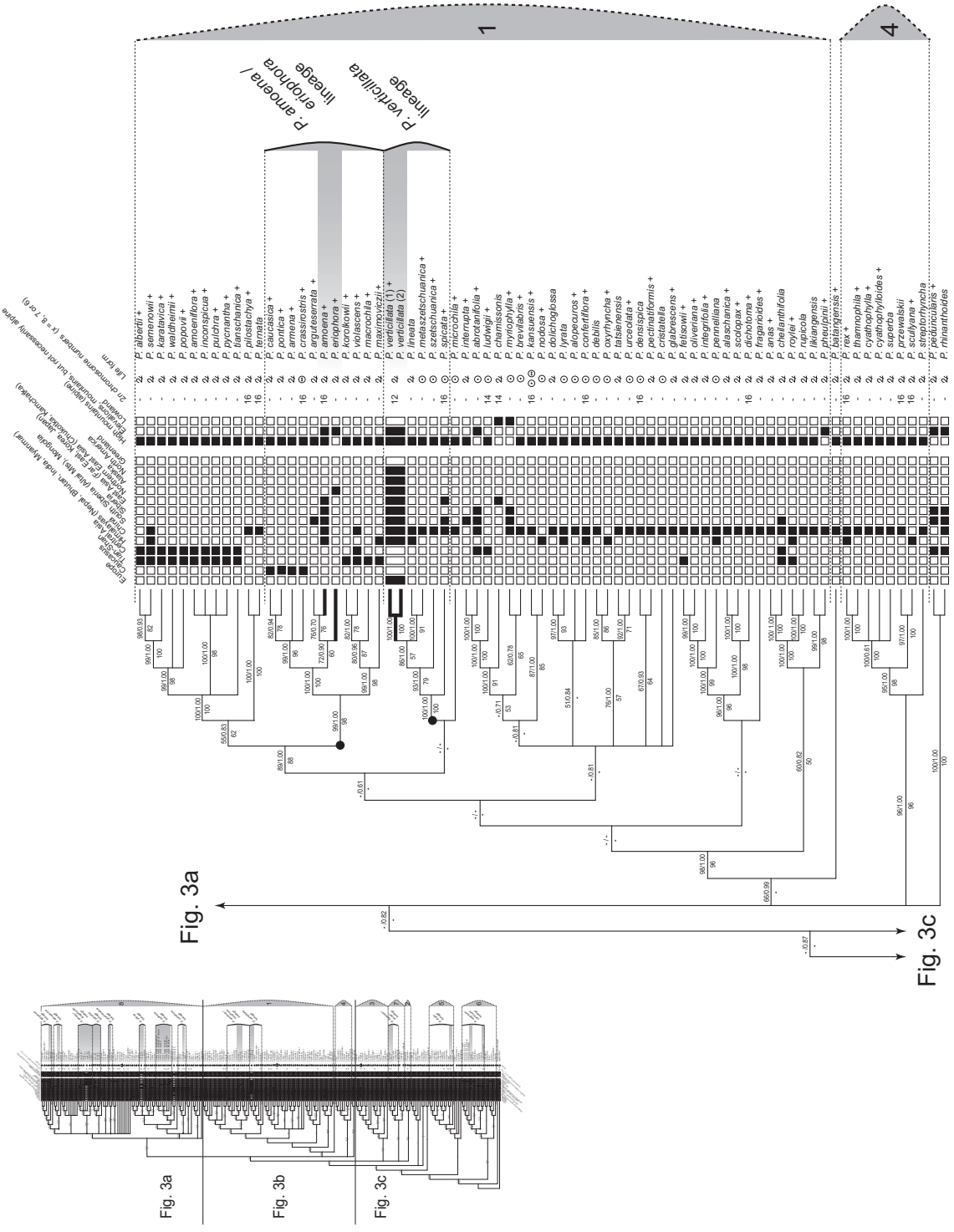

Fig. 3 (*continued*)

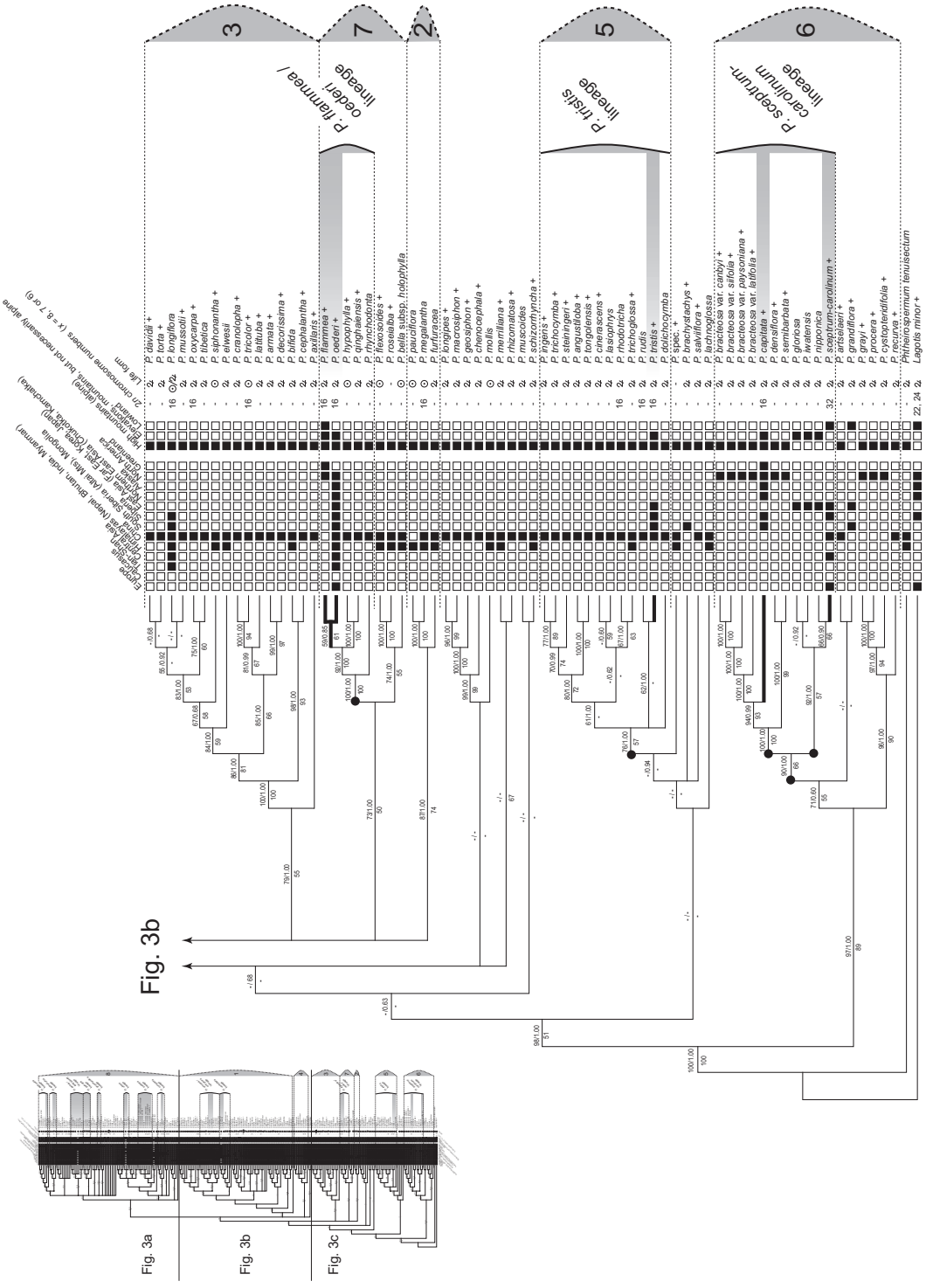
3
7
2
5
6
P. flammea / oederi lineage
P. tristis lineage
P. scaptrum-calolimum lineage
Fig. 3b
Fig. 3a
Fig. 3c
P. davidii +
P. torta +
P. longiflora
P. mussotii +
P. oxycarpa +
P. tibetica
P. sphaeroantha +
P. elwesii
P. cranolopha +
P. tricolor +
P. latituba +
P. armata +
P. decorissima +
P. bifida
P. cephalantha +
P. agleniis +
P. flammea +
P. oederi +
P. hypophylla +
P. qinghaiensis +
P. rhynchodonta
P. flexosoides +
P. roseialba +
P. beiii subsp. hobphylla
P. paucifiora
P. meeboldiana
P. turfanensis
P. longipes +
P. macrosiphon +
P. geosiphon +
P. chenocephala +
P. mollis
P. merrilliana +
P. rhizomatosa +
P. muscoides
P. schizocalycha +
P. ingens +
P. trichocymba +
P. steiningeri +
P. angustiloba +
P. tongolensis +
P. cinerascens +
P. lasiophrys
P. rhodochlora
P. trichoglossa +
P. tristis +
P. dulcichcymba
P. spec. +
P. brachystachys +
P. salviiflora +
P. lechnoglossa
P. bracteosa var. canbyi +
P. bracteosa var. sirifolia +
P. bracteosa var. paryophora +
P. bracteosa var. latiloba +
P. capitata +
P. densiflora +
P. semibarbata +
P. gloriosa
P. iwatensis
P. nipponica
P. scaptrum-carolinum +
P. artselaeri +
P. groenlandica +
P. grayi +
P. procera +
P. cystopteridifolia +
P. recurva +
Phtheirospermum tenuisectum
Lagotis minor +
Life form
21n chromosome numbers but not necessarily alpine
Habit (herbaceous [alpine], rosulate [alpine], Cowherd - Rosulate [Subscapose] Hemiparasite)
Habitat (Alpine [Alpine Meadow], Alpine [Alpine Scree], Alpine [Alpine Scree (Nepal Bhutan India Myanmar)], Alpine [Alpine Scree (Tibet Xizang)], Alpine [Alpine Scree (Yunnan)], Alpine [Alpine Scree (Yunnan Sichuan)], Alpine [Alpine Scree (Yunnan Sichuan Xizang)], Alpine [Alpine Scree (Yunnan Xizang)], Alpine [Alpine Scree (Yunnan)], Alpine [Alpine Scree (Yunnan)], Alpine [Alpine Scree (Yunnan

Table 3
Sister group comparison of arctic and non-arctic *Pedicularis* for soil moisture preferences and altitudinal distribution of arctic taxa outside the Arctic.

Lineage, sub-clade (if applicable)	Number of arctic taxa	Number of non-arctic taxa	Soil moisture preferences			Lowland/high mountain distribution of arctic taxa outside the Arctic
			Arctic taxa	Non-arctic taxa	Differences between arctic and non-arctic taxa	
P. sceptrum-carolinum, *P. sceptrum-carolinum*	1	3	Wet	Wet	No	Lowland
P. sceptrum-carolinum, *P. capitata*	1	6	Mesic	Mesic	No	High mountain
P. tristis	1	11	Wet	Mesic	Yes?	High mountain
P. flammea/oederi	2	6	Mesic	Mesic	No	High mountain
P. verticillata	1	4	Indifferent	Indifferent	No	High mountain
P. amoena/eriophora	2	9	Mesic	Mesic	No	High mountain
P. compacta	1	2	Wet (not salty)	Wet (salty) (4)	No	High mountain
P. sudetica	7	1	Wet (*P. pacifica*: dry)	Dry	Yes?	High mountain
P. villosa (1)	1	1	Dry	Dry	No	n.a.
P. groenlandica	1	1	Wet	Wet	No	High mountain
P. palustris (2)	4	0	Wet	n.a.	n.a.	Lowland
P. lanata/langsdorffii (2)	7	0	Wet or mesic (3)	n.a.	n.a.	High mountain
P. labradorica	1	3	Indifferent	Indifferent	No	High mountain
P. lapponica	1	5	Wet	Wet	No	High mountain

Notes: (1) compared with *P. schistostegia*, (2) clade comprises only arctic taxa, comparison not possible, (3) wet-dry differentiation within the arctic clade, (4) occurrence on salty soils may be an apomorphy of the non-arctic sister taxa, n.a. – not applicable.

The North American sub-lineage within the *Pedicularis sceptrum-carolinum* lineage comprised the widespread and also north-east Asian arctic *P. capitata* as well as some western American species. All species occur in high mountain areas. Two species (*P. densiflora* and *P. semibarbata*) grow under rather dry conditions in oak or conifer forests and their openings. The occurrence in dry habitats appears to be a novel ecological character, because all other species of the *Pedicularis sceptrum-carolinum* lineage are found in moist habitats (Table 3). *Pedicularis bracteosa* grows in moist forests and meadows in the montane belt of the Rocky Mountains. *Pedicularis capitata* seems to prefer mesic conditions on pingos or elevations of the arctic plains. Outside of the Arctic it mostly occurs above the tree line. Seemingly due to its adaptation to colder conditions, *P. capitata* occupies a much larger range than the non-arctic relatives. The yellow-flowered *P. capitata* has a denser indumentum than the non-arctic species with yellow or red flowers (Table 4).

Glabrous and yellow-flowered *P. sceptrum-carolinum* is widespread in Eurasia and grows throughout its range in bogs and other wet places. The species is nested within a lineage comprising species endemic to Japan and the Eurasian Far East that are also growing in moist to wet habitats of lowlands. They have red flowers and a dense indumentum. The origin of the Japanese endemics (*P. gloriosa*, *P. iwatensis*, *P. nipponica*) from continental ancestors (Fujii, 2007) was supported by this study (Fig. 3).

3.3.2. Pedicularis tristis lineage

Pedicularis tristis occupies an Asian range extending from the Arctic southwards to the Altai Mountains and eastwards along the mountains to the Russian Far East and China. The eleven other species of the *P. tristis* lineage are high mountain endemics of China. They mostly occur on grassy slopes and alpine meadows, whereas *P. tristis* grows in rather dry tundra habitats, but also in wet and boggy meadows and willow scrub. According to the data available, *P. tristis* is significantly smaller than its sisters but has larger flowers (Table 4).

3.3.3. Pedicularis flammea/oederi lineage

Pedicularis flammea occurs from north-western Canada to Iceland as well as in a small area of northern Norway. *Pedicularis oederi* ranges from southern Norway through the European high mountains and Eurasia to Alaska. The two species are almost completely allopatric with overlap restricted to parts of Alberta (Canada) from where *P. albertae* was described. Outside the Arctic both species are confined to the alpine zone. Even in the Arctic they seem to prefer mountains or at least hills (Hultén, 1968; Pospelova and Pospelov, 2007). Both species form a well-supported lineage (100/1.00/100) nested within endemic species from China that are confined to the areas above the tree line (Fig. 3). Widespread and arctic *P. flammea* and *P. oederi* have seemingly originated from predecessors occurring in southern high mountains. With respect

Table 4
Comparison of arctic taxa and their non-arctic relatives for the scored morphological traits.

Lineage, sub-clade (if applicable)	Life form	Indumentum	Flower color (3)	Plant height	Corolla length
P. sceptrum-carolinum, *P. sceptrum-carolinum*	=	A: glabrous, NA: hairy	A: yellow, NA: red	–	–
P. sceptrum-carolinum, *P. capitata*	=	A: densely hairy, NA: loosely hairy	A: yellow, NA: yellow/red	–	–
P. tristis	=	||	||	A < NA ($p = 0.02$)	A > NA ($p = 0.01$)
P. flammea/oederi	||	||	||	–	–
P. verticillata	||	||	=	–	–
P. amoena/eriophora	=	||	||	–	–
P. compacta	=	A: glabrous, NA: hairy	||	–	–
P. sudetica	=	||	=	–	–
P. villosa (1)	=	=	A: red, NA: yellow	–	A < NA (4)
P. groenlandica	=	A: glabrous, NA: hairy	=	–	A < NA (4)
P. palustris (2)	=	=	=	n.a.	n.a.
P. lanata/langsdorffii (2)	=	||	=	n.a.	n.a.
P. labradorica	A: annual, NA: perennial	||	A: both, NA: yellow	–	–
P. lapponica	=	=	||	–	–

Notes: A – arctic taxa, NA – non-arctic taxa, = – no difference between arctic and non-arctic taxa, || – character states overlapping between arctic and non-arctic taxa, (1) compared with *P. schistostegia*, (2) clade comprises only arctic taxa, comparison not possible, (3) base color, both indicate that yellow/white and red flowers occur, (4) only two species, n.a. – not applicable.

to their ecology and scored morphological characters, *P. oederi* and *P. flammea* apparently underwent no major changes relative to their non-arctic allies.

3.3.4. Pedicularis verticillata lineage

Pedicularis verticillata occupies a wide range extending from the European high mountains through Eurasia and Alaska to western Canada. The phylogeny suggests that *P. verticillata* originated from species growing in China and adjacent territories (Russian Far East, southern Siberia, Bhutan, Nepal). It has a wide ecological amplitude and grows in fairly dry meadows and tundra but also in wet and boggy meadows, characters that are shared with the non-arctic species of the *P. verticillata* clade (Fig. 3).

3.3.5. Pedicularis amoena/eriophora lineage

Arctic *P. amoena* and *P. eriophora* are nested within a lineage of high mountain species of Asia. This clade comprises two well-supported sub-clades. The non-arctic taxa of the first sub-clade (99/1.00/98) are distributed in the Tian Shan Mountains and occur in alpine meadows and on stony slopes. The second sub-clade (100/1.00/100) includes *P. amoena*, *P. eriophora*, and five further species from the Caucasus and adjacent mountain areas. The species are also restricted to high elevations and occur in similar habitats. The ranges of *P. eriophora* and *P. amoena* are almost allopatric. *Pedicularis eriophora* is confined to high mountains of the Russian Far East (Kamchatka range, Okhotskiy, and Koryakskiy range), whereas *P. amoena* is widely distributed from Chukotka to the Ural Mountains and has a large range in the Central Asian and southern Siberian high mountains. It is sister to *P. arguteserrata*, endemic to southern Siberian and northern Mongolian high mountains. In terms of ecology and the studied morphological characters no significant differences between arctic and non-arctic taxa were found (Table 4).

3.3.6. Pedicularis compacta lineage

Arctic *P. compacta* grouped with three non-arctic species. Its non-arctic range encompasses the southern Siberian and Mongolian mountains. In this region *P. compacta* mostly grows above the tree line. *Pedicularis compacta* prefers moist to wet and not salty places throughout its range, whereas the non-arctic relatives grow frequently in salty meadows and steppes. Morphologically, *P. compacta* differs from them by having glabrous stems.

3.3.7. Pedicularis villosa lineage

The placement of P. villosa, a subendemic arctic species, within Clade 8 was ambiguous (see Section 3.1). Pedicularis villosa is a tetraploid species ($2n = 32$) and an allotetraploid hybrid origin might account for the different placements in the trees. The species prefers dry tundra and meadows, sandy or stony coast, and river borders. In the combined tree, red-flowered and small P. villosa is sister to yellow-flowered and tall P. schistostegia with northern East Asian distribution.

3.3.8. Pedicularis sudetica lineage

The *Pedicularis sudetica* complex consisted of morphologically similar taxa that were recognized in different floras as subspecies or separate species (Ivanina, 1991; Molau and Murray, 1996; Elven et al., 2011). The relationships of the studied taxa were not well resolved in the molecular phylogenetic tree, suggesting a recent diversification. The taxa are mostly confined to the Arctic, where they occupy partly allopatric ranges. Outside the Arctic, they occur in southern Siberian and North American high mountains as well as in eastern Central Europe (*P. sudetica* s. str.). The plants prefer wet meadows or shrub formations, bogs or swamps. The eastern Rocky Mountains species *P. scopulorum* was sister to the *P. sudetica* complex. *Pedicularis scopulorum* occurs in Wyoming, Colorado, and New Mexico and seemingly prefers drier habitats such as rocky or stony alpine meadows, a character shared with arctic *P. sudetica* subsp. *pacifica*.

3.3.9. Pedicularis palustris lineage

This lineage comprised four species that are generally restricted to the Arctic except for the Eurasian *P. palustris* (including *P. karoi*). The species prefer moist and wet habitats such as bogs and swamps. The Beringian region is the center of diversity of this clade. All species are annuals or biennials.

3.3.10. Pedicularis groenlandica lineage

This lineage was part of the large polytomy in Clade 8 and comprised only two American species, *P. attollens* and *P. groenlandica*. These species have a galea with a very long and upwards bent beak, and were placed sometimes in the separate genus *Elephantella* Rydb. The glabrous arctic species *P. groenlandica* occurs from the south-western Rocky Mountains northwards to Alaska and eastwards to Greenland, whereas the non-arctic, hairy, and larger-flowered *P. attollens* is restricted to the Rocky Mountains of California, Nevada, and Oregon. Both species thus have allopatric distribution. They prefer wet and open habitats and are found in the South in moderate to high altitude (Cronquist, 1959).

3.3.11. Pedicularis lanata/langsdorffii lineage

This well-supported lineage consisted exclusively of perennial arctic species. Comparable to the *P. palustris* lineage, its center of diversity is situated in the Beringian region, with some species extending their ranges to the southern Siberian mountains (*P. alopecuroides*, *P. hirsuta*) or the Rocky Mountains (*P. langsdorffii*, *P. lanata*). Species of this clade are ecologically varied since *P. langsdorffii* and *P. hirsuta* prefer wet or boggy meadows, the other, usually densely hairy species dry and stony tundra.

3.3.12. Pedicularis labradorica lineage

Biennial arctic *P. labradorica* is widespread from the Ural Mountains East through Beringia to the northern Atlantic coast of North America and Greenland. It is quite abundant in the North and found in different tundra habitats ranging from almost peaty to dry soils. The perennial, non-arctic species of the *P. labradorica* clade are distributed in the Russian Far East and Japan and occur prevailingly in high mountains.

3.3.13. Pedicularis lapponica lineage

Pedicularis lapponica has a circumpolar arctic distribution extending to the Altai, the Sayan Mountains of southern Siberia and northern Mongolia, and Scandinavia. *Pedicularis labradorica* has a similar distribution and both are absent only from western Eurasia. *Pedicularis lapponica* seems to prefer moist to wet habitats. The sister species of *P. lapponica* occur in North America from Mexico (*P. angustifolia*) to Canada (*P. canadensis*).

3.4. Geographical distribution, habitat, life form, and chromosome numbers of arctic Pedicularis

The distribution ranges of the arctic taxa are generally larger than those of their non-arctic sisters (Fig. 3). Sizes and geographical locations of the ranges are highly varied in arctic *Pedicularis* (Table 3, Fig. 3). Many species have large distribution ranges in the Arctic with only a few non-arctic occurrences, e.g., *P. lapponica* and *P. capitata*. In other species the major part of the range lies outside and only the minor part within the Arctic, e.g., *P. palustris*, *P. tristis*. Only four taxa are confined to small and exclusively arctic areas, these are *P. sudetica* subspp. *arctoeuropaea* and *gymnostachya*, *P. villosa*, *P. dasyantha*. Outside the Arctic, most arctic *Pedicularis* species have their distribution ranges in high mountain areas. Only the species of

the *P. palustris* lineage and *P. sceptrum-carolinum* with its relatives occur within and outside the Arctic in lowland areas.

Nearly all species of the arctic lineages prefer wet to moist soil conditions with the exception of the *P. tristis* lineage. Ecological variation is encountered also within the *P. sudetica* lineage by the arctic *P. sudetica* subsp. *pacifica* and the non-arctic *P. scopulorum*.

The chromosome base number of the genus *Pedicularis* is predominantly $x = 8$, rarely $x = 7$ (*P. ludwigii*, *P. chamissonis*) or $x = 6$ (*P. verticillata*). Most *Pedicularis* species were reported to be diploid. The arctic taxa are diploids with the exception of the tetraploids *P. sceptrum-carolinum*, *P. villosa*, and *P. sudetica* subsp. *gymnostachya*. The latter was sometimes merged with diploid *P. sudetica* subsp. *interior*.

Arctic and non-arctic sister taxa have no consistently different morphological characters (Table 4). Most *Pedicularis* taxa of the Arctic are perennials. Exceptions are (1) the *P. labradorica* lineage, in which the arctic biennial *P. labradorica* clustered together with perennial non-arctic taxa, and (2) the *P. palustris* lineage consisting exclusively of annual and biennial species. In the *P. sceptrum-carolinum*, *P. groenlandica,* and *P. compacta* lineages hairy non-arctic taxa are opposed to glabrous arctic relatives. *Pedicularis capitata* is densely hairy, whereas the non-arctic relatives are only loosely hairy.

Plant height of arctic and non-arctic sister taxa were almost always similar (mid-range values and minimum values). *Pedicularis tristis* is the only example of an arctic species that is significantly ($p = 0.011$) smaller than its non-arctic relatives. Arctic and non-arctic taxa differ in flower color, but no consistent pattern was found. Corolla sizes differ between arctic and non-arctic taxa in four lineages (Table 4). The arctic taxa have larger flowers than the non-arctic in the lineages of *P. tristis* and *P. groenlandica*, whereas they are smaller in the lineages of *P. compacta* and *P. villosa*.

4. Discussion

4.1. Phylogenetics and biogeographical patterns of Pedicularis

The taxonomy of *Pedicularis* is complicated due the regional restricted species selection and due to different and barely comparable approaches of evaluating morphological characters. Vvedensky (1955) in the Flora SSSR focussed on floral traits, whereas other, e.g., Li (1948, 1949) and Tsoong (1955, 1956) dealing mainly with Chinese species, used mostly vegetative traits for classification. These classifications were elaborated almost simultaneously and the authors became late aware of this. Li's work was not known to Vvedensky when preparing his account (Vvedensky, 1955: p. 688) nor was Vvedensky's treatment later known to Tsoong, who became aware of it only when the second part of his own *Pedicularis* classification was in press (Tsoong, 1956: p. 43).

The comparison of the sections and series in *Pedicularis* circumscribed by Vvedensky (1955), Li (1948, 1949), and Tsoong (1956) with the molecular phylogenetic results of this study revealed that most of their groups were para- and polyphyletic. This impeded the usage of traditional classifications for the inference of the provenance of arctic species. Species not available for the molecular studies that were considered by the above-mentioned authors to be closely related to our target species could thus, unfortunately, not be included in morphological and biogeographical analyses.

The molecular phylogenetic tree revealed (at least) eight major clades, most of which were basically in accordance with clades identified by Ree (2005). Clades 7 and 8 were new because of our extended sampling of many European, Central Asian, and North American species. This clades agreed to some extent with the taxonomical treatment of Vvedensky (1955) in the Flora SSSR.

The eight clades of *Pedicularis* reflect the general biogeographical diversification patterns of the genus. Species of the early diverging Clade 6 occur predominantly in North America and/or in East Asia. The species of Clades 1–5, 7 concentrate on the diversity hot spot of the genus, the Hengduan Mountains of south-western China and the Himalayas (Ree, 2005). For this area a high number of endemic but also species with wider distribution were reported. Species of Clade 8, conversely, are absent from this region. This clade comprises species from Europe, North America, but also from northern and Central Asia. Except for Clade 8, only the most widespread arctic species are represented also in Europe (*P. sceptrum-carolinum*, *P. oederi*, *P. verticillata*).

4.2. Origin of arctic Pedicularis

North-temperate high mountains were frequently suggested to be a main source of arctic species (Hedberg, 1992; Hultén, 1937, 1958; Tolmachev, 1960; Weber, 1965). In *Ranunculus* we found this origin only in one of nine lineages (Hoffmann et al., 2010), although some non-arctic lineages consisted of many alpine species. In *Artemisia*, another genus with many species in the Arctic, an unambiguous high mountain origin of arctic taxa could not be inferred, even though many species occur in high mountains (Tkach et al., 2008a, 2008b). This implies that high numbers of alpine species in genera may be advantageous for a successful colonization of the Arctic but is not necessarily a requisite.

In *Pedicularis* we observed 13 arctic lineages, implying 12–14 independent colonizations or immigrations of the northernmost regions. This pattern was found also in other arctic genera such as *Artemisia* (Asteraceae, 13–18 independent colonzations; Tkach et al., 2008a, 2008b), *Ranunculus* (Ranunculaceae, at least 13 times; Hoffmann et al., 2010), *Cardamine* (Brassicaceae, at least 9 times; Carlsen et al., 2009). Most of the arctic *Pedicularis* taxa were nested within lineages comprising species of southern high mountains. In this genus, the long-standing hypothesis of high mountain origin of arctic species was supported by molecular phylogenetic results.

The present centers of *Pedicularis* diversity in south-western China and the adjacent Himalayas appear be the cradles for three arctic lineages: *P. flammea/oederi*, *P. tristis,* and *P. verticillata*. A common feature of these lineages is that all non-arctic members are largely restricted to the Hengduan Mountain region, while only their arctic species have considerably larger ranges. This suggested a high mountain origin of these arctic lineages in south-western China. Causes of these range expansions were not readily apparent. Adaptation to cold environments seems unlikely, because all species of these lineages are growing in high mountains and thus should be equally adapted to environmental conditions comparable to the Arctic (see Section 1).

A second example of high mountain origin refers to the Caucasus, Tian Shan, and adjacent high mountains of Central Asia, from where the arctic sister species *P. amoena* and *P. eriophora* most likely originated. A northern East Asian mountain origin seems to apply to *P. labradorica* and *P. lapponica*. Their non-arctic sister taxa are distributed in the mountains of Japan, Siberia, and the Russian Far East.

Probably also of Asian mountain origin were *P. compacta*, *P. villosa*, and the arctic taxa of the *P. sudetica* lineage. They belonged to a fully supported sub-clade of Clade 8, whose members are distributed in northern Eurasia. High mountain origin of the arctic species is likely, because the non-arctic relatives of this sub-clade grow frequently, though not consistently in high mountain habitats.

Pedicularis capitata and *P. groenlandica* had North American origin, but presumably did not stem from high mountain regions, because their non-arctic sister taxa occur mainly in the forest belt of the Rocky Mountains. This contrast the high mountain origin of many Asian taxa as discussed above, whose sister species are confined to the vegetation above the tree line.

Lowland origins of arctic species could be inferred only for *P. palustris* and *P. sceptrum-carolinum*. The latter species most likely originated in East Asia, whereas the geographical provenance of

two arctic lineages (*P. palustris* and *P. lanata/langsdorffii*) was less clear. These lineages appeared to be closely related to American taxa, which might imply a North American origin of these groups. The arctic Beringian region is the centre of the diversity for both lineages, indicative of a northern diversification not encountered in any other lineage of *Pedicularis*.

In situ evolution of arctic species was likely in *Pedicularis* by *P. eriophora* and *P. villosa*, because the two species are nearly confined to the Arctic and their sisters are arctic species. Arctic *in situ* speciation has also been documented, for example, in *Artemisia*, *Cerastium*, *Douglasia*, *Draba*, *Ranunculus*, and *Saxifraga* (e.g., Brochmann et al., 1998; Grundt et al., 2006; Hoffmann et al., 2010; Jørgensen et al., 2006; Scheen et al., 2004; Schneeweiss et al., 2004; Tkach et al., 2008a, 2008b).

4.3. Trait evolution in arctic Pedicularis

Soil moisture preferences of *Pedicularis* species showed marked phylogenetic niche conservatism (Ackerly, 2003; Crisp and Cook, 2012). Most species occur in mesic to wet habitats, only some species are confined to rather dry conditions, for example, *P. densiflora* in California and Oregon (Vorobik, 2012). A few species may grow in salty soils, like *P. altaica* (Vydrina, 1996). Most arctic taxa of *Pedicularis* retain the ecological characteristics of their non-arctic relatives in terms of soil moisture preferences (Table 3), indicating considerable niche conservatism. Niche evolution of arctic taxa in relation to their sisters was encountered in the *P. tristis* lineage, in which the arctic species *P. tristis* occupies wetter habitats than its relatives. This shift had possibly enabled the range expansion of *P. tristis* across the northern hemisphere, because wetlands are very widespread in the Arctic and thus suitable for the species (Walker et al., 2005). The arctic species of other studied genera like *Artemisia* and *Ranunculus* also showed this extensive niche conservatism for soil moisture content (Tkach et al., 2008a, 2008b; Hoffmann et al., 2010). Arctic species of *Pedicularis* and *Ranunculus* frequently were derived from phylogenetic lineages already adapted to moist, boggy, or even aquatic habitats in *Ranunculus*. By contrast, *Artemisia* is a genus of mainly dry to mesic habitats, like dry tundra and steppes. Such preferences to drier soils were conserved even in arctic species of *Artemisia*.

Annual and biennial life forms are rare in the arctic flora (Gussarova et al., 2012; Savile, 1972) and might be considered to be disadvantageous in the unstable arctic environmental conditions. Short-lived arctic species were observed, for example, in the families Polygonaceae (*Koenigia islandica*), Portulacaceae (*Montia fontana*), Primulaceae (*Androsace septentrionalis*), Asteraceae (*Tephroseris palustris*), and Gentianaceae (*Gentianella aurea*). With the exception of the Gentianaceae (more than seven short-lived arctic taxa), these native arctic species are the single representatives of their families in the Arctic. These families are otherwise rich in short-lived species and have also many arctic perennial species.

Four of seven hemiparasitic genera of the plant family Orobanchaceae reported for the Arctic (*Euphrasia*, *Melampyrum*, *Pedicularis*, *Rhinanthus*) comprise many annuals and biennials. In *Pedicularis* five arctic taxa are short-lived annuals and biennial, the remaining 25 arctic *Pedicularis* taxa are perennials. The *P. palustris* lineage has consistently annual and biennial arctic species. For *P. labradorica*, a biennial species nested in the phylogenetic tree within perennial species of the Asian Far East, the evolution of the biennial life cycle may be linked with the occupation of a larger range including the Arctic. *Euphrasia* is represented in the Arctic by 13 species (Elven et al., 2011), all of which are annuals, whereas non-arctic *Euphrasia* species have annual and perennial life cycles. The molecularly studied annual representatives of this genus in the Arctic have annual sisters in European high mountains (Gussarova et al., 2012). It may be possible that the hemiparasitism of the Orobanchaceae has enabled many short-lived species to grow in the Arctic (more than 20 arctic short-lived species in total).

Several changes in plant morphology were considered to be associated with the occupation of arctic environments. These include smaller plant size, prostrate growth form, formation of cushions, and larger flowers (e.g., Archibold, 1995; Savile, 1972; Tikhomirov, 1963). In *Artemisia*, the arctic taxa are significantly smaller than the non-arctic sisters and have larger flowering heads (Tkach et al., 2008a), whereas no changes in plant size, flower size, or growth form occurred in *Ranunculus* (Hoffmann et al., 2010). In *Pedicularis* we found no consistent pattern of morphological changes between arctic and non-arctic taxa, for example, with respect to the hairiness of stems, flower sizes or plant height. Considering the frequent high mountain origin of the arctic taxa, this inconsistent pattern may be attributed to adaptations already evolved during the occupation of alpine regions.

The occupation of arctic habitats was frequently considered to be associated with polyploidy (Brochmann and Steen, 1999; Brochmann et al., 2004; Jordon-Thaden and Koch, 2008). In *Artemisia* and *Ranunculus* diploid and polyploid species occur in the Arctic. The ploidal level is phylogenetically conserved in these genera. If arctic taxa are polyploid, then also their non-arctic relatives are polyploid (Hoffmann et al., 2010; Tkach et al., 2008a). Only three polyploid species are known in *Pedicularis*, all of which occur in the Arctic (Goldblatt and Johnson, 1979–forthcoming), these are the widespread Eurasian *P. sceptrum-carolinum*, as well as *P. villosa* and *P. sudetica* subsp. *gymnostachya* in the Arctic of the Russian Far East. Ivanina (1980) argued that the latter two taxa originated by polyploidy and their restricted distribution ranges in the Arctic actually suggested *in situ* origin. Most of the arctic *Pedicularis*, however, are diploid and occupy large distribution ranges (e.g., *P. palustris*, *P. oederi*, *P. groenlandica*). Although all known polyploid *Pedicularis* occur in the Arctic, polyploidization has apparently not initiated a particular diversification of the genus in the Arctic.

5. Conclusions

We studied more than 200 species including all but one arctic species of *Pedicularis* in a phylogenetic context. The molecular phylogeny revealed 13 lineages with arctic taxa. The Arctic was colonized 12–14 times independently. High mountain origin of arctic taxa, a long-standing biogeographical hypothesis on taxon recruitment of this biome, could be verified in *Pedicularis*. However, this is not the only pathway of arctic species origin found in this genus. The evolution of arctic *Pedicularis* did not follow a uniform pattern, which is reflected also by the other morphological, ecological, cytogenetic, and biogeographical characteristics scored.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ympev.2014.03.004.

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